

Stable isotopes, functional morphology, and human evolution: a model of consilience

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Received _____; accepted _____

ABSTRACT

Foraging behaviors are constrained in part by the energy within resources, as well as the mechanical costs of procuring and consuming them. Molar enamel thickness is a morphological trait that differentiates African apes from hominins, being manifested most dramatically among hominins with large (megadont) molars and hyperthick enamel (e.g. *Paranthropus* spp.). Among primates, thicker enamel correlates with the consumption of stiffer, deformation-resistant foods, probably because thicker enamel can better resist cracking under high compressive loads. Accordingly, plant underground storage organs (USOs) are thought to be a central food resource for early hominins, in part due to their accessibility and mechanical characteristics. However the potential effects of this putative foraging behavior on enamel wear has received little attention. Here we present a process-based model to investigate foraging constraints as a function of energetic demands and enamel wear among anthropoid primates. Our framework allows us to explore if and under what conditions stiff foods such as USOs are chosen as fallback, rather than preferred, resources. Moreover, we quantify the potential fitness benefits of extradentary processing or the direct employment of megadont molars on mechanically stiff USOs. Our model predictions bring consilience, or at least offer a plausible resolution, to the noted disparity between hominin isotopic and microwear dietary evidence.

Subject headings: Hominin evolution, Enamel thickness, *Paranthropus*, Foraging models, Underground Storage Organs, Fallback foods

Introduction

26

All animals must acquire and deliver food to their digestive systems. The mechanics
28 of this process can result in the gradual wear, or senescence, of anatomical structures
such as claws, beaks, and teeth. Such wear is detrimental to the foraging efficiency and
30 reproductive success of a wide range of animals (Swennen et al. 1983; Raupp 1985; Juanes
1992; Juanes and Smith 1995; Roitberg et al. 2005; King et al. 2005). For mammals, the
32 oral processing, or chewing, of food is a necessary wear-inducing behavior (Stirling 1969;
McArthur and Sanson 1988; Skogland 1988; Perez-Barberia and Gordon 1998), and natural
34 selection is expected to favor dental attributes that prolong chewing efficiency. Accordingly,
considerable attention has been focused on the microstructure, morphology, and functional
36 ecology of mammalian molars, particularly the enamel.

Enamel is a hard, mineralized tissue covering the elastic and vascularized dentin, and
38 rooted by cementum to the jaws of most mammals (Lucas 2004). Oral comminution of food
prior to digestion is, today, a uniquely mammalian behavior (Lucas 2004), although gizzards
40 and pharyngeal teeth can serve this function in birds and some teleosts, respectively, and
some ornithischian dinosaurs did comminute food orally (Weishampel et al. 2004). Some
42 mammals have ever-growing teeth, but primates replace their molar teeth only once, after
which they face an adult life of wear and occasional catastrophic damage (Constantino
44 et al. 2010). Thus, adult primates must find a balance between the opposing advantages of
enamel preservation and the consumption of foods with different propensities for enamel
46 wear. In this vein, the identification of contemporary form-function relationships between
tooth enamel and diet have been instructive for inferring foraging behavior in the fossil
48 record, and dental enamel has long informed debate in the discipline of paleoanthropology
(Ungar and Sponheimer 2011).

50 For example, among living mammals, relatively thick molar enamel is widely associated

with the consumption of stiff, deformation-resistant (hard) foods, and it follows that
 52 hominins such as the genus *Paranthropus*, which possessed large ‘megadont’ molars with
 hyperthick enamel, also consumed such foods (Kay 1981, 1985; Lucas et al. 2008*b,a*; Vogel
 54 et al. 2008; Wood and Constantino 2007; McGraw and Daegling 2012; McGraw et al. 2012;
 Wood and Schroer 2012; Constantino 2013) Yet, the identity of these stiff food objects
 56 has long puzzled researchers and fueled hypotheses on the cost of dietary specialization
 (Balter et al. 2012). More recently, isotopic data have emerged from a range of hominin
 58 taxa, including *Paranthropus*, that reveal a heavy dependence on C₄-photosynthetic
 plants (which have tissues enriched in ¹³C and include tropical grasses and sedges) or
 60 possibly animals that consumed these plants (Sponheimer and Lee-Thorp 1999; Ungar and
 Sponheimer 2011). Depending on the tissue, C₄ plants can be highly resistant to fracture or
 62 deformation, mechanical attributes that are expected to induce wear or chip the enamel of
 molar teeth. Indeed, the molars of *Paranthropus boisei* are often heavily worn and deeply
 64 chipped (Constantino et al. 2010); and yet, paradoxically, the occlusal surfaces of seven
 well-preserved molars evince a microwear fabric that indicates a diet of soft, pliable foods
 66 (Ungar et al. 2008, 2010). These discrepant lines of evidence - indicating a diet of C₄
 foods that are simultaneously hard and soft - have been challenging to reconcile, and it is
 68 sometimes referred to as the C₄ conundrum.

For *Paranthropus*, the consumption of ¹³C-enriched tissues might have included
 70 graminivorous insects and/or the leaves, seeds, and underground storage organs (USOs) of
 grasses and sedges (Sponheimer and Lee-Thorp 2003; Sponheimer et al. 2005; Yeakel et al.
 72 2007; Cerling et al. 2011; Lee-Thorp 2011). Recently, the USOs - bulbs, corms, and rhizomes
 - of grasses and sedges have attracted special attention (Dominy 2012; Lee-Thorp et al.
 74 2012) because they are widespread in many savanna habitats and a central food resource
 for some populations of baboons and humans (Post 1982; Barton et al. 1993; Youngblood
 76 2004; Alberts et al. 2005). Corms in particular are stiff and deformation-resistant (Dominy

et al. 2008) and a significant cause of tooth wear among savanna baboons (Galbany et al.
78 2011). Yet the mechanical and nutritional properties of these potential foods, as well as
the anatomical constraints of hominin dentition, are seldom factored into interpretations of
80 hominin foraging behavior, and the diet of *Paranthropus* remains obscured by disquieting
discrepancies (Grine et al. 2012). Here we attempt to bring consilience to these discrepancies
82 with a model-based approach.

The physiological and behavioral processes that yield inconsistent interpretations
84 of diet arise can be explored with foraging models that depend on the anatomical and
energetic states of potential foragers. Here we present a Stochastic Dynamic Programming
86 (SDP) model (Mangel and Clark 1988; Mangel and Ludwig 1992; Houston and McNamara
1999; Clark and Mangel 2000) to quantify the optimal foraging decisions for organisms that
88 must balance energetic gain with enamel wear, while accounting for the stochastic effects of
a variable environment. We establish our model on measurements for anthropoid primates
90 and focus specifically on decisions affecting hominins in savanna-woodland environments.
We determine decision matrices in which specific food resources are chosen to maximize an
92 animal’s fitness, conditional on two internal states: the organism’s energetic reserves and
molar enamel volume.

94 This model-based approach is well-suited to test a variety of important questions about
the effects of dental enamel on foraging, and we focus on three potentially informative
96 lines of inquiry. First, and most essential, how does the quantity of enamel influence the
foraging strategies of savanna-woodland anthropoid primates, and how does megadont
98 dentition alter these strategies? Second, to what degree do these foraging decisions depend
on resource quality and quantity, where the quality and quantity of particular food items
100 can vary depending on the environmental conditions? Third, can extradentary mechanical
advantages, such as peeling, pounding, or cooking alter the influence of dental enamel, and

to what extent do these alterations provide fitness benefits? Finally, we relate our model predictions to paleontological evidence of hominin diets, and conclude by showing that the model framework presented here can be used to both predict and update paleodietary data.

Methods

Model Architecture

State variables: We model the foraging decisions of an organism as a function of two principle state variables: 1) the organism’s net energy reserves at time t , $X(t) = x$, and 2) the organism’s enamel volume at time t , $V(t) = v$, where time is measured in days. The net energy reserves of an organism determine the amount of energy available to it for basal metabolic costs and daily energetic expenditures (e.g. foraging). We model a single unit of energy as 10 Megajoules [MJ], equivalent to 2388 kcal and roughly equal to the energy in 1 kg of animal tissue (Wolfram Research 2012). Accordingly, the maximum potential energy reserves for an organism, x_{\max} , is its body size, such that $x_{\max} = 70$ for a 70 kg organism, and a change in x by a single value is a change of 10 MJ. Because an organism cannot use all of the energy contained in its mass, we set a critical threshold for an organism’s energy reserves ($x_{\text{crit}} = (3/4)x_{\max}$) below which it cannot survive. By contrast, a unit of molar enamel volume v corresponds to 100 mm³ (approximately equivalent to a sphere with a 2.9 mm radius). Among anthropoids, specific properties of molar anatomy correlate strongly with body size, and these properties can be used to approximate maximal (i.e. unworn) molar enamel volume, v_{\max} as a function of x_{\max} (see appendix I, fig. S1).

Mechanical properties: The potential energy gained from food, as well as its impact on an organism’s enamel, changes as a function of food mechanical properties. Here we consider an approximating measurement for the mechanical properties of food that takes

into account both the elasticity (Young’s modulus, E_i , [MPa]) and the fracture toughness
 126 (R_i , [Jm^{-2}]) of food i , and is generally assumed to approximate ‘hardness’, measured as
 $\sqrt{E_i R_i}$ (Lucas et al. 2008b). Moreover, the toughness of a food is proportional to the
 128 amount of fiber (Lucas et al. 2000). We let η_i denote the digestibility of food i ranging
 between $\eta_i = 0$ (indigestible) and $\eta_i = 1$ (completely digestible).

130 *Gains:* For food type i , an organism’s energetic gains are denoted as γ_i (in units
 of x). We identify four general food groups: 1) a nutritious, mechanically pliable,
 132 patchily distributed food (e.g. fruit), 2) a non-nutritious, mechanically hard, widely
 distributed food (e.g. grass leaves), 3) a moderately nutritious, mechanically hard, widely
 134 distributed food (e.g. USOs), and 4) a highly-nutritious, potentially hard, patchily
 distributed food (e.g. arthropods or more generally small quantities of animal tissue).
 136 We set the food energy density to be 717, 150, 785, and 1518 kcal/kg for fruit, grass
 leaves, USOs, and arthropods/animal tissue (Wolfram Research 2012). Because larger
 138 animals gain relatively more calories per foraging bout, energetic gain is calculated as
 $\gamma_i = (\text{energy density}/2388) \cdot (x_{\text{max}}/10)$, where the constant $(1/2388)$ normalizes the energy
 140 density of foods to units of x , and the modifier $(x_{\text{max}}/10)$ ensures that gain scales weakly
 with increasing body size. Although we acknowledge that macromolecules such as protein
 142 are vital for growth and differentiable from basic energetic requirements, here we assume
 that foraging behavior is primarily governed by caloric, or energetic, limitations (Rothman
 144 et al. 2011).

Costs: We model the daily cost of foraging for food type i , c_i (in units of x), as
 146 a function of an organism’s body size, and the aggregation of food on the landscape.
 Foraging costs increase nonlinearly with body size, such that larger organisms spend a
 148 smaller fraction of energy per unit time than do smaller organisms. We modified the
 allometric relationship proposed by Leonard and Robertson (1997) to model daily energetic

cost (kcal/day), such that $c_i = C_1 \cdot \text{RMR} \cdot (1/\xi_i)/2388$, and Resting Metabolic Rate is $\text{RMR} = 69.1x_{\text{max}}^{0.761}$, where C_1 is the activity constant ($C_1 = 3.80$ for moderate activity), the constant ($1/2388$) operates as before, and ξ_i is the mean encounter rate for food i , such that $(1/\xi_i)$ is proportional to foraging time. Therefore, foods that are encountered more frequently (high ξ_i) have lower per encounter foraging costs. In addition, we assessed a second, costlier, version of the model, where $c_i = (C_1 \cdot \text{RMR} \cdot (1/\xi_i) + C_2 \cdot \text{RMR})/2388$, where $C_2 = 1.2$, accounting for additional daily costs independent of food choice (Leonard and Robertson 1997).

Mechanical Advantage: Extradentary mechanical advantages are introduced when an organism modifies the mechanical properties of a particular food resource. If an organism is incapable of altering the mechanical properties of food other than by chewing, we model the organism as having no mechanical advantage. Accordingly, values for toughness [Jm^{-2}] are $R = (561, 300, 265, 1345)$, and Young’s modulus [MPa] are $E = (1, 11, 5, 200)$ for fruits, grass leaves, USOs, and arthropods, respectively (Lucas 2004; Williams et al. 2005; Dominy et al. 2008). We note that the high value of R for arthropods is due to their fracture resistant exoskeletons.

Many animals, and primates in particular, can modify the mechanical properties of foods before they are consumed (Altmann 2009). We consider three potential extradentary mechanical advantages: 1) the peeling, pounding, or cooking of USOs, ($R_{\text{USO}} = 138$ and $E_{\text{USO}} = 5$; Dominy et al. 2008), 2) the peeling of arthropod exoskeletons ($R_{\text{arthropod}} = 306$ and $E_{\text{arthropod}} = 0.22$) (alternatively, this mechanical advantage can account for swallowing arthropods with minimal chewing), and 3) a combination of mechanically altering both USOs and arthropods.

Habitat Quality: The quality of a habitat at a given time, $Q(t)$, is variable, and this affects both the nutritional gains and foraging costs of foods. We model habitat quality

to be rich ($Q(t) = r$) or poor ($Q(t) = p$) at time t , such that habitat quality $Q(t)$ changes
 176 through time in accordance to a transition probability matrix ($\boldsymbol{\rho}$) where

$$\boldsymbol{\rho} = \begin{pmatrix} \rho_{rr} & \rho_{rp} \\ \rho_{pr} & \rho_{pp} \end{pmatrix}, \quad (1)$$

and, for example, ρ_{rp} is the probability of transitioning from a rich quality habitat at time
 178 t to a poor quality habitat at time $t + 1$. The differences between rich and poor quality
 habitats are defined by differences in energetic gain, the mean encounter rate, and the
 180 dispersion of different foods. We set energetic gain to decrease by 10% in poor quality
 habitats relative to rich quality habitats. Moreover, the mean encounter rate (ξ_i) as well as
 182 the dispersion of food (ν_i) are modified by $Q(t)$, such that food resources are more easily
 found (higher ξ_i) and are less patchily distributed (higher ν_i) in rich quality habitats (see
 184 appendix II for a detailed derivation of dispersion and encounter rates of foods). USOs
 are stored underground and have evolved to retain high nutrient loads during periods of
 186 environmental stress (Copeland 2004). We incorporate this quality by holding the energetic
 gain, encounter rate, and dispersion of USOs constant, irrespective of habitat quality.
 188 Accordingly, habitat quality influences both food quality (in terms of its energetic gain),
 as well as the risk associated with finding food (in terms of its mean encounter rate and
 190 dispersion).

With this basic framework, we can assess the influence of ‘wet’, ‘dry’, and ‘autocorrelated’
 192 environmental conditions on foraging decisions. Wet environments have high values of
 ρ_{rr} , ρ_{pr} , and low values of ρ_{rp} , ρ_{pp} (such that habitat quality is generally rich). Dry
 194 environments have low values of ρ_{rr} , ρ_{pr} , and high values of ρ_{rp} , ρ_{pp} (such that habitat
 quality is generally poor). Autocorrelated environments are likely to have habitats that
 196 stay rich (if they are rich) or stay poor (if they are poor), and thus have high values of
 ρ_{rr} , ρ_{pp} , and low values of ρ_{rp} , ρ_{pr} (see table 1). We recognize that natural systems are

more idiosyncratic, however this simplification allows us to assess the effects of changing habitat quality over time with minimal added complexity.

State Dynamics

The random variable K represents the number of food items found in a single foraging period and that with probability $f_K(k)_i$ an individual finds k items of food type i . We maintain this notation, upper case for random variables and lower case for specific values, for all stochastic variables. Because an organism’s daily consumption is limited by gut volume, daily caloric gain is bounded by $x_s = (1/5) \cdot x_{\max}$ (proportional to average anthropoid % gut volume; Milton 1989). This bound functions only to limit the energetic gain in the event a large amount of food (high k) is found during a foraging period. Thus, an organism’s energy reserves change according to the difference equation

$$X(t+1) = X(t) + \min(k\eta_i\gamma_i, x_s) - c_i. \quad (2)$$

Enamel volume steadily decreases as an animal consumes resources. Although the underlying mechanisms of enamel loss are poorly understood (Lucas et al. 2008a), siliceous particulate matter is probably the most significant cause of abrasion (Lucas et al. 2012). Here we assume that hard foods (high $\sqrt{E_i R_i}$ values) promote increased use of the dentition (cf. Organ et al. 2011), and that such use induces wear regardless of the specific cause. Accordingly, we set enamel wear, $\Delta v(\Omega)$, to be a function of: 1) the mechanical properties of food i and 2) a stochastic decrease in enamel volume (determined by Ω). Because enamel is a nonrenewable resource, this wear cannot be undone. Teafor and Oyen (1989) showed that the consumption time for vervet monkeys (*Chlorocebus*) that ate a diet of raw Purina monkey chow was 8x greater than that for vervets fed on pre-mashed monkey chow. With

respect to enamel wear, this is equivalent to chewing 8x as much food. Teafor and Oyen
 220 also showed that the enamel thickness decreased by ca. $0.58 \mu\text{m day}^{-1}$ when vervets fed on
 the raw diet, versus ca. $0.24 \mu\text{m day}^{-1}$ when they fed on the pre-mashed diet. We assumed
 222 a linear relationship between the loss of enamel thickness (from Teafor and Oyen 1989),
 and consumption time, or, alternatively, the amount of food consumed, k (with a slope
 224 $b = 0.0425$). The lower-bound of this relationship ($\bar{\omega} = 0.24 \mu\text{m}$) represents the expected
 basal enamel wear that occurs irrespective of consumption, and is used to parameterize
 226 the stochastic variable Ω . Accordingly, given that A is the molar enamel surface area and
 E_{MC} and R_{MC} are scaling constants denoting the average Young’s modulus (50.44 MPa)
 228 and fracture toughness (1030.55 Jm^{-2}) of monkey chow, respectively (Williams et al. 2005),
 enamel volume changes according to the difference equation

$$V(t+1) = V(t) - \underbrace{\frac{A}{250} \left(\frac{bk\sqrt{E_i R_i}}{\sqrt{E_{MC} R_{MC}}} + \Omega \right)}_{\Delta v(\Omega)}. \quad (3)$$

230 The constant $1/250$ scales tooth wear to ensure the organism attains its expected longevity
 (Lindstedt and Calder III 1981), and accounts for 1) overestimation of molar enamel area
 232 (our allometric estimation includes the lateral aspects of molar surfaces), and 2) the notion
 that wear is a complex action affecting a small fraction of the occlusal surface at a given
 234 time (Lucas 2004).

The basal loss of enamel thickness has an expected value $E(\Omega) = \bar{\omega} = 0.24 \mu\text{m}$. As
 236 such, chewing and the daily wear unassociated with chewing (Lucas 2004) have variable
 effects on enamel wear. Specifically, enamel wear is typically small, but occasionally large,
 238 and is realized when the organism chips or loses a tooth or part of a tooth (cf. Boccara
 2004). We model the probability that Ω falls within the small interval ω and $\omega + d\omega$ as a
 240 lognormal distribution, such that

$$\begin{aligned}
 f_{\Omega}(\omega) &= \text{LogNormal}(\omega|\bar{\omega}, \sigma) \\
 &= \frac{1}{\omega\sigma\sqrt{2\pi}} \exp\left(-\frac{(\ln \omega - \bar{\omega})^2}{2\sigma^2}\right),
 \end{aligned} \tag{4}$$

where $E(\Omega) = \bar{\omega}$ and $\text{Var}(\Omega) = \sigma^2$ (see table 1). We assume that an individual dies when
 242 its energy reserves fall below x_{crit} or its enamel volume falls below v_{crit} .

The Fitness Function

244 We consider a nonbreeding interval of length T during which only foraging decisions
 influence fitness. This interval will ultimately become sufficiently large (see below) so that
 246 we can use decisions that are independent of time (cf. Mangel and Clark 1988; Clark and
 Mangel 2000), and assume that at the end of this interval, the fitness of an individual with
 248 energy reserves x and enamel volume v is $\Phi(x, v)$. For numerical computations we use

$$\begin{aligned}
 \Phi(x, v) &= \frac{1}{2} \left(2 - \frac{x_{\text{crit}}}{x} - \frac{v_{\text{crit}}}{v} \right), \quad \text{where } \begin{cases} x > x_{\text{crit}} \\ v > v_{\text{crit}} \end{cases}, \\
 \Phi(x, v) &= 0, \quad \text{otherwise.}
 \end{aligned} \tag{5}$$

The maximum fitness at $t = T$ is realized by an organism with $X(T) = x_{\text{max}}$ and
 250 $V(T) = v_{\text{max}}$, and the rate of fitness decline increases as x and v approach x_{crit} and v_{crit} .
 We explored alternatives such as $\Phi(x, v) = (1 - \frac{x_{\text{crit}}}{x})(1 - \frac{v_{\text{crit}}}{v})$ and they had little effect on
 252 the qualitative predictions. We scaled the terminal fitness function to be 1, so it is easiest
 to consider it as survival after T for an individual whose end state is $X(T) = x, V(T) = v$.

254 As described above, we also consider alternative environmental conditions (wet, dry,
 and autocorrelated), which differ in the probabilities of transitioning between rich and poor

256 quality conditions. We assume that natural selection has acted on behavioral decisions
concerning diet (food choice) conditioned on physiological and environmental states. We
258 define fitness functions

$$F_r(x, v, t) = \max_i E \{ \Phi(X(T), V(T)) | X(t) = x, V(t) = v, Q(t) = r \}, \quad (6a)$$

$$F_p(x, v, t) = \max_i E \{ \Phi(X(T), V(T)) | X(t) = x, V(t) = v, Q(t) = p \}, \quad (6b)$$

where the maximization over i chooses the food that maximizes fitness given energy
260 reserves, enamel volume, and environment. By definition, at time T

$$F_r(x, v, T) = F_p(x, v, T) = \Phi(x, v).$$

Maximizing Fitness by Food Choice

262 For time periods before the terminal time $t = T$, an organism must survive mortality
independent of starvation or enamel loss and choose the fitness maximizing food, given
264 the stochasticity in food encounter. If the probability of death in a single period is set
to $m \approx e^{-10}$, (estimated for a subadult male chimpanzee; cf. Bronikowski et al. 2011),
266 then $F_r(x, v, T)$ and $F_p(x, v, T)$ satisfy the equations of Stochastic Dynamic Programming

(SDP), such that

$$F_r(x, v, t) = \max_i (1 - m) \left(\sum_{k=0}^{k_{max}} f(k_r)_i \left(\rho_{rr} E_{\Omega} \{ F_r(x_r + \min(k\eta_i\gamma_i, x_s)_r - (c_i)_r, v - \Delta v(\Omega), t + 1) \} \right. \right. \\ \left. \left. + \rho_{rp} E_{\Omega} \{ F_p(x_r + \min(k\eta_i\gamma_i, x_s)_r - (c_i)_r, v - \Delta v(\Omega), t + 1) \} \right) \right), \quad (7a)$$

$$F_p(x, v, t) = \max_i (1 - m) \left(\sum_{k=0}^{k_{max}} f(k_p)_i \left(\rho_{pr} E_{\Omega} \{ F_r(x_p + \min(k\eta_i\gamma_i, x_s)_p - (c_i)_p, v - \Delta v(\Omega), t + 1) \} \right. \right. \\ \left. \left. + \rho_{pp} E_{\Omega} \{ F_p(x_p + \min(k\eta_i\gamma_i, x_s)_p - (c_i)_p, v - \Delta v(\Omega), t + 1) \} \right) \right), \quad (7b)$$

where the expectation E_{Ω} is with respect to the random variable Ω (eq. 3). These equations identify the food i that maximizes fitness for a given energetic reserves $X(t) = x$, enamel volume $V(t) = v$, and habitat quality $Q(t)$ at time t . Thus, optimal food selection takes into account the probabilistic quantities of finding K items of food i , (from the frequency distribution $f_K(k)_i$; see appendix II) and losing a basal amount of enamel volume Ω , (from the frequency distribution $f_{\Omega}(\omega)$), as well as the probability that the environment remains in its current state or changes according to the transition probability matrix $\boldsymbol{\rho}$. As eqns. 7 are solved backward in time, in addition to obtaining the values of fitness, we create decision matrices $D_r(x, v, t)$ and $D_p(x, v, t)$ characterizing the optimal choice of food in a rich or poor environment given that $X(t) = x$ and $V(t) = v$. Thus, two decision matrices are solved for three environmental scenarios determined by the habitat quality transition matrix $\boldsymbol{\rho}$: 1) Wet: where habitat quality is generally rich, 2) Dry: where habitat quality is generally poor, and 3) Autocorrelated: where habitat quality shifts similarly between rich and poor, but tends to remain in its current state.

The Stationary Solutions

As t moves backwards further and further away from T the fitness maximizing decisions become independent of time and depend only upon state, which accords with the intuition that far from the time at which fitness is assessed, the behavior of an organism is expected to depend on its state and on the environment, but not on the current time. We used these stationary decisions, which we denote by $D_r^*(x, v)$ and $D_p^*(x, v)$ for further analysis. We confirmed stationarity by calculating the summed square differences between decision matrix solutions from $t + 1$ to t , such that $\Delta D(t) = \sum_{v,x} (D(x, v, t + 1) - D(x, v, t))^2$, for $t = T - 1$ to $t \ll T$ and we assumed stationary decisions had been reached when $\Delta D(t) \rightarrow 0$ for $t \ll T$ (for an example, see fig. S2).

Forward Iteration

The stationary solutions to the dynamic programming equations, $D_r^*(x, v)$ and $D_p^*(x, v)$, identify foods that maximize fitness for a given state (x, v) in both rich quality ($Q = r$) and poor quality ($Q = p$) habitats. We used a forward iteration algorithm (Mangel and Clark 1988; Clark and Mangel 2000) to assess the impact that these foraging decisions have on the expected future fitness of individuals by iteratively solving for the state dynamics of simulated foragers over time, as specified by the state dynamics in eqns. 2 and 3. At each time τ , the n^{th} simulated individual, with states $X_n(\tau)$ and $V_n(\tau)$ forages for the food i determined by the decision matrices $D_r^*(X_n(\tau), V_n(\tau))$ and $D_p^*(X_n(\tau), V_n(\tau))$, and whether habitat quality is rich or poor. The time variable τ is used to denote forward-iterated time units experienced by simulated individuals making foraging decisions in accordance to the stationary decision matrices, as opposed to the time units t used to calculate stationary decision matrices.

To test whether and to what extent mechanical advantages conveyed fitness benefits to hominin primates, we quantified expected future fitness, $\hat{F}(\tau|D^*, Q(\tau))$, for $n = 1, 2, \dots, N = 100$, 50 kg individuals, with maximal foraging costs for days $\tau = 1$ to $\tau_{\max} = 10950$ (expected lifespan of 30 years) given both the stationary decision solutions and habitat quality. As energy reserves and/or enamel volume decrease over the lifetime of an individual, \hat{F} is expected to decrease similarly. We quantified the expected future fitness at time τ of a population, given rich or poor habitat quality, as

$$\hat{F}(\tau|D^*, Q(\tau)) = \frac{1}{N} \sum_{n=1}^N F^*(X_n(\tau), V_n(\tau)|D^*, Q(\tau)). \quad (8)$$

Characterizing the Megadont Advantage

We explored the potential adaptive benefits of megadont dentition using two approaches. First, we compared the proportions of foods identified to maximize fitness in accordance to the stationary decision solutions $D_r^*(x, v)$ and $D_p^*(x, v)$. Organisms that are predicted to utilize a particular resource across a greater proportion of states (x, v) may have fitness benefits in environments where those resources are plentiful. However, although the percentage of foraging choices in decision matrices is an efficient summary of potential dietary behavior, it should not be viewed as the proportional contribution of food to an individual’s diet over time, which is calculated with the forward iteration algorithm.

To determine whether megadont dentition provided fitness benefits over the lifetime of an individual organism, we compared expected future fitness, \hat{F} , for populations of individuals with and without megadont dental anatomy, and during both wet environments (where rich quality habitats are more likely) and dry environments (where poor quality habitats are more likely).

Results

The stationary solutions to the Stochastic Dynamic Programming equations predict that energy reserves and enamel volume have large consequences for diet choice. For animals without mechanical advantage in rich quality habitats, foods with the energetic and mechanical properties of fruit maximize fitness for all potential states (x, v) (fig. 1A). In poor quality habitats, fruits maximize fitness only if energy reserves were high (fig. 1B); as reserves decline the optimal resource switches from fruit to plant USOs. Plant USOs confer less energetic gain than fruit, but this is mitigated by reduced foraging risk due to a more even spatial distribution (high dispersion, ν). As enamel volume declined with age, the mechanical hardness of USOs, which produced greater enamel wear, promoted an increased reliance on riskier but mechanically pliable foods such as fruit.

Because foraging costs scaled nonlinearly with body size, optimal foraging decisions varied accordingly. For larger animals and for each environmental scenario in our model (wet, dry, and autocorrelated), a poor habitat quality was strongly associated with the consumption of riskier foods with higher nutritional yields such as fruit, whereas low quality, ubiquitous foods such as USOs were an important supplement (fig. 2A). Animals with smaller body sizes tended to rely on USOs exclusively. When habitat quality was rich, both smaller- and larger-bodied animals switched to a diet of energy dense foods (fruit). In the absence of extradentary mechanical advantages, extremely energy dense, but relatively rare foods such as arthropods were not consumed by animals of any size, regardless of habitat quality. For all mechanical advantage scenarios, as body size increased the role of plant USOs remained constant, however arthropods (highest nutritional gain and lowest probability of encounter) were favored over fruit (fig. 2). Thus, in both rich and poor quality habitats, large-bodied anthropoid primates increased the percentage of extremely risky foods, such as arthropods, if their mechanical properties could be altered to preserve

enamel (fig. S3). Smaller-bodied animals lacked the energetic reserves required to forage on
 352 rare, but energy dense foods such as arthropods, regardless of their mechanical advantages.

In poor quality habitats, stationary decision matrices reveal that megadont hominins
 354 could maximize fitness by incorporating a relatively greater proportion of fracture resistant
 foods. With no mechanical advantage, megadont decision matrices show a reduction in the
 356 percentage of fruit, and an increase in fracture-resistant USOs relative to non-megadonts
 (fig. 3). As mechanical advantages are introduced, megadont decision matrices show
 358 similar percentages of each food item as those of non-megadonts with one important
 difference. Regardless of the mechanical advantage, megadont decision matrices have a
 360 greater percentage of USOs.

For all populations, forward iterations revealed that expected future fitness decreased
 362 sharply early in life, but saturated as the population reached its expected lifespan of 30
 years (10950 days) (fig. 4). Our results point to an important difference between the
 364 three mechanical advantage scenarios that are considered (none, arthropods, arthropods
 + USOs; because the decision matrices for the USO mechanical advantage was nearly
 366 identical to the no mechanical advantage scenario, for simplicity we show only forward
 equation results for the latter) (fig. 4A,B; solid lines). Although the decision matrices for
 368 the arthropod and arthropod + USO scenarios are similar for non-megadont primates, these
 mechanical advantages appear to have large impacts on expected fitness. For both wet and
 370 dry environmental conditions, having either mechanical advantage provides large fitness
 benefits, but the difference in fitness *between* mechanical advantages is small, particularly
 372 when habitat quality is generally rich (wet conditions).

The fitness benefits of megadont dentition are more obvious. Megadont populations
 374 have greater expected future fitness than those of non-megadonts - irrespective of mechanical
 advantage - and these differences are more exaggerated later in life (fig. 4A,B; stippled

lines). The predicted fitness benefits generated by mechanical advantage are generally less for megadont populations than for non-megadont populations.

Discussion

Although model-based approaches have been used to investigate the foraging strategies of humans (Belovsky 1988), nonhuman primates (Boyer et al. 2006; Sayers et al. 2010), and even the interactions between the two (Levi et al. 2011), few have been applied to extinct primates (but see Dunbar 2005; Janssen et al. 2007; Griffith and Long 2010), and none have taken into account nonrenewable resources such as dental enamel. This omission is surprising given the functional significance prescribed to molar morphology, and its known impact on dietary behavior. Stochastic Dynamic Programming models demand the explicit expression of processes determining fitness, as well as sources of external and internal stochasticity (Mangel and Clark 1988; Clark and Mangel 2000). Our goal here is not to create an agent-based demographic model of anthropoid foraging behavior (cf. Griffith and Long 2010), but to assess directly the dependence of diet choice on enamel volume, and to quantify the extent that attributes such as extradentary mechanical advantage or megadont dentition alter predicted foraging behaviors.

Body Size and the Role of Fallback Foods

An important and counterintuitive result from our model concerns the effect of body size in poor quality habitats. We found that smaller body sizes can rely exclusively on USOs, whereas larger body sizes can subsist on a greater proportion of fruit in tandem with a smaller proportion of USOs. Such a result highlights the spatial and temporal ubiquity of USOs compared to fruit, and it suggests that the abundance and predictability of a

398 food resource matters more to smaller, predator-sensitive consumers with relatively higher
metabolic demands. Perhaps compellingly, this result is compatible with the high degree
400 of sexual size dimorphism observed in *Paranthropus robustus* - males are substantially
larger than females - which suggests reduced food competition between females and intense
402 male-male competition for access to females (Lockwood et al. 2007). Such social behavior
is manifested most strongly when predation risk is high and food resources are common
404 and widespread. Thus, for larger-bodied males, a diet premised on USOs is predicted to
be suboptimal, but males are unlikely to abandon their monopolization of smaller-bodied
406 females. As a result, males are expected to be more susceptible to predation due to poorer
body condition; indeed, evidence suggests that males are disproportionately overrepresented
408 in predator-accumulated fossil assemblages (Lockwood et al. 2007).

Multiple lines of evidence suggest that plant USOs were important foods for early
410 hominins. Plants with geophytic structures are both diverse and abundant in arid habitats
(Pate and Dixon 1982; Vincent 1985; Procheş et al. 2006), and modern hunter-gatherers
412 utilize these resources extensively, particularly in marginal environments (Marlowe 2003;
Marlowe and Berbesque 2009). Associations between mole rats - known USO specialists -
414 and hominins suggest that human ancestors lived in USO-abundant habitats (Laden and
Wrangham 2005), while stable isotope analysis of both modern and fossil mole rats confirm
416 that USO specialists have isotopic values similar to those of *Australopithecus africanus*
and *Paranthropus robustus* (Yeakel et al. 2007). It has widely assumed that USOs served
418 as fallback rather than preferred foods due to their lower nutritional content and relative
availability (Schoeninger et al. 2001). The results of our model are in general agreement
420 with this assumption, but show that the role of USOs as fallback foods varies - in part - as
a function of an organism’s energy reserves, enamel volume, and body size.

422 In general, the consumption of USOs is predicted if enamel volume is relatively high

and energy reserves are relatively low (fig. 1). However, our model also predicts a tradeoff
 424 with respect to the role of USOs as fallback foods as body size is altered. Smaller-sized
 animals tend to preferentially use nutritious foods such as fruit in rich quality habitats and
 426 less nutritious but more ubiquitous foods such as USOs in poor quality habitats (fig. 2A).
 Thus, as energetic reserves become more limiting, as they are for smaller organisms with
 428 relatively higher resting metabolic rates, fruit and USOs alternatively serve as preferred
 foods when habitat quality is rich and poor, respectively. Larger body size enables risky
 430 foraging on fruits even when habitat quality is poor. In this case, larger animals resort to
 USO consumption when energy reserves are low. Accordingly, USOs are relegated to a
 432 fallback status, and are consumed if the act of foraging for preferred foods incurs relatively
 greater fitness costs on the organism. Factors such as increased digestive efficiency are
 434 expected to counterbalance the benefits of risky foraging for very large animals, and the
 advantages these adaptations provide could be explored using a SDP approach.

436 Although hominins are expected to have less complex hind-gut fermenting digestive
 physiologies (Milton 1989), they were likely capable of mechanically altering their food prior
 438 to consumption, and others had megadont dentition that likely facilitated consumption of
 fracture resistant foods. We find that both mechanical advantages and megadont dentition
 440 strongly affect predicted foraging behavior. Physically altering the mechanical properties
 of resources increases potential dietary diversity by decreasing the fitness costs of fracture
 442 resistant foods. In general, the mechanical advantages (USOs, arthropods, and arthropods
 + USOs) all increase the proportion of higher risk foods, particularly for large body sizes,
 444 in the predicted decision matrices $D_r^*(x, v)$ and $D_p^*(x, v)$ (fig. 2B,C,D). Under the USO
 mechanical advantage, the percentage of USOs increased only marginally, while that of
 446 fruit declined. By comparison, the introduction of an arthropod or arthropod + USO
 mechanical advantage altered the decision matrices considerably. The increase in arthropod
 448 consumption was limited to organisms with larger body size, the result of larger animals

having both energetic reserves and enamel volume to spare, factors that decrease the risk
of obtaining rare or patchily distributed food that tend to be fracture resistant.

It stands to reason that the evolution of megadont dentition, which increases the
quantity of enamel volume for a given body size, may serve a similar function. Megadont
dentition was a prominent morphological feature of robust hominins, though its fitness
benefits are a source of contention. Megadont hominins ranged from 2.5 to 1.1 Ma, had
smaller incisors and canines, and molars with hyperthick enamel (Shellis et al. 1998; Lucas
et al. 2008a). Such extreme molar enamel thickness would have increased tolerance of
fracture resistant foods (Kay 1981; Osborne 1981; Macho 1999) and it is hypothesized
to have evolved in response to hard-object feeding, possibly on grass seeds (Jolly 1970)
or plant USOs (Laden and Wrangham 2005; Sponheimer et al. 2005; Yeakel et al. 2007;
Dominy et al. 2008). Our model predicts that fracture resistant foods maximize fitness for
a relatively greater proportion of internal states (x, v) for megadont hominins (fig. 3). This
morphological adaptation may have been competitively advantageous in stressed or poor
quality habitats where fracture resistant foods are relatively more abundant.

The Fitness Benefits of Mechanical Advantage and Megadont Dentition

Both extradentary mechanical advantages and megadont dentition increase the
nutritional benefits of fracture resistant foods and provide fitness advantages to hominins
in poor habitat quality environments. Expected future fitness changes over an individual’s
lifetime, and is expected to diverge as enamel wears at different rates. Our process-based
model is simplistic in that life-history stages are not included, however these simplifications
enable a number of predictions regarding hominin foraging behavior: 1) behaviors that
alter the mechanical properties of fracture resistant foods result in greater fitness; 2)
these benefits are primarily realized in dry environments (where habitat quality is more

likely to be poor), where fracture resistant foods are relatively more abundant; 3) because
474 megadont dentition results in relatively slower wear rates, megadonts have greater expected
fitness than non-megadonts, but these benefits are primarily realized later in life. Our
476 understanding of hominin diets is informed by many lines of evidence including dental
morphology, molar microwear, and the stable isotope ratios of tooth enamel. We have
478 shown that different foraging choices are predicted to maximize fitness among non-megadont
and megadont hominins, and that these foraging strategies have different expected lifetime
480 fitness values. We next show how a forward iteration approach can be used to examine
the isotopic differences observed among hominin species, and whether the mechanical and
482 physiological constraints imposed by our model are predictive of the isotopic patterns
observed in the fossil record.

484 Plants that use C₃- and C₄-photosynthetic pathways have different ratios of stable
carbon isotopes (¹³C/¹²C). These isotopic ratios are recorded in consumer tissues and can
486 be used to quantify the proportions of isotopically distinct resources in a consumer’s diet.
Animals that consume C₃ plants (e.g. shrubs and trees) tend to be more depleted in ¹³C
488 (low $\delta^{13}\text{C}$ values; where $R = ^{13}\text{C}/^{12}\text{C}$ and $\delta^{13}\text{C} = 1000((R_{\text{sample}}/R_{\text{standard}}) - 1)$, with units of
per-mil, ‰), while those consuming C₄ plants (e.g. tropical grasses and sedges) tend to be
490 less depleted in ¹³C (high $\delta^{13}\text{C}$ values) (Koch 2007). Here and henceforth, we refer to the
 $\delta^{13}\text{C}$ values of carbonate, the mineral component of bone and tooth enamel. Megadont (*P.*
492 *robustus* and *P. boisei*), as well as some non-megadont hominins (*A. africanus*), have tissues
with relatively high $\delta^{13}\text{C}$ values (Sponheimer and Lee-Thorp 1999; Ungar and Sponheimer
494 2011), suggesting that they were consuming either large quantities of C₄ plants or animals
that ate C₄ plants. These findings are at odds with evidence from dental microwear, which
496 tend to support consumption of non-fracture resistant, pliable foods (Ungar et al. 2008,
2010; Ungar and Sponheimer 2011).

Using the forward equation framework presented above, if each food choice has an associated distribution of $\delta^{13}\text{C}$ values, we can explore under what conditions the accumulated $\delta^{13}\text{C}$ value of an individual within a population changes over time as a function of its energetic reserves, enamel volume, and the prevailing environmental conditions (see appendix III for details). Our results show that the $\delta^{13}\text{C}$ values of a simulated population of $N = 100$, 50 kg anthropoid foragers capable of mechanically altering both arthropods and USOs is influenced by both energetic reserves and enamel volume. In dry environments and where foraging costs are minimal, the mean $\delta^{13}\text{C}$ value of simulated foragers remains relatively high ($\delta^{13}\text{C}_{\text{avg}} \approx -10.5\text{‰}$; fig. 5A), due to a greater reliance on USOs (fig. S3). After day 3500, $\delta^{13}\text{C}_{\text{avg}}$ declines to -11.2‰ as the proportional contribution of USOs decreases and that of fruits increases (fig. 5B). This highlights the increasing importance of foods that are less fracture resistant as enamel is worn - despite greater energetic costs - as well as the accompanying decrease in the mean $\delta^{13}\text{C}$ value of a consumer population over its lifespan.

If foraging costs are too great, low risk, fracture resistant foods are preferred despite greater enamel wear, resulting in a higher $\delta^{13}\text{C}_{\text{avg}} \approx -8.8\text{‰}$ (fig. 5C). In this case, our model predicts $\delta^{13}\text{C}$ values equivalent with those observed for *A. africanus* and *P. robustus* (Ungar and Sponheimer 2011). In costlier environments (where energetic cost includes both foraging costs as well as daily costs independent of food choice), USOs tend to maximize fitness (fig. 5D) until late in life, when the risks of foraging pliable but rare foods are superseded by those associated with declining enamel volume.

These results help resolve the observed discrepancy between hominin isotopic ratios and molar microwear. Molar enamel is formed early in life (Lucas 2004) when food selection tends towards fracture resistant foods with high $\delta^{13}\text{C}$ values. As enamel is worn, softer, less abundant foods with lower $\delta^{13}\text{C}$ values maximize fitness (fig. 5A,B). Because fossilized

microwear is formed shortly before death (the ‘last supper effect’), our model results suggest
 524 that softer, less fracture-resistant foods will have a disproportionately large influence on
 the microwear of teeth, particularly for older individuals. In both cases, simulated foragers
 526 incorporated foods in proportions that are not predicted by their relative abundance on
 the landscape, highlighting the importance of considering both mechanical and energetic
 528 constraints in addition to resource abundance when constructing prior distributions for
 isotopic studies.

For example, our model does not show C₄ grass leaves to be solutions to the SDP for
 530 either non-megadont or megadont hominins (fig. 3), despite the high relative abundance
 532 of this resource. This accords well with the aversion to C₄ plants observed among
 savanna-dwelling chimpanzees (Sponheimer et al. 2006) and some hominin species including
 534 *Ardipithecus ramidus* (White et al. 2009) and *Australopithecus sediba* (Henry et al. 2012).
 Despite their relative availability, C₄ plants tend to be more fracture resistant (Boutton
 536 et al. 1978) and less nutritious (Barbehenn et al. 2004), possibly due to the presence of
 bundle sheath cells. Similar mechanisms have been cited to explain the avoidance of C₄
 538 plants by herbaceous insects in grassland communities (Caswell et al. 1973; Boutton et al.
 1978; Pinder III and Kroh 1987). However, megadont hominins such as *P. boisei* have $\delta^{13}\text{C}$
 540 values $\approx 0\text{‰}$, which corresponds to a diet of 75-80% C₄ foods (Ungar and Sponheimer
 2011). Such a heavy dependence on C₄ foods has led to speculation that *P. boisei* was
 542 possibly a grazing hominin (Lee-Thorp 2011; Rabenold and Pearson 2011), an extraordinary
 idea that begs the question: under what circumstances could C₄ grass leaves maximize
 544 fitness?

We found that when fracture resistant, low risk, and low calorie foods are hyper-
 546 abundant (such that the encounter rate of grass leaves, ξ_{grass} , is increased from 4 to 5; cf.
 table 1), they were represented in both non-megadont and megadont decision matrices

(fig. 6A,B), the consumption of C₄ grasses was a fallback behavior *in extremis*, selected only when enamel volume was high and energy reserves were extremely low. Moreover, megadont dentition led to a greater percentage of states where grass leaves maximize fitness relative to non-megadonts (fig. 6B), and this is in accordance with the elevated $\delta^{13}\text{C}$ values observed for megadonts such as *P. boisei*.

Foraging behaviors are a consequence of both the mechanical and energetic costs of food and the constraints imposed by an organism’s dentition. Dental enamel thickness is a highly conserved trait among individuals within modern human populations (Lucas et al. 2008*b*), yet it varies considerably across hominin lineages in the fossil record. This variability is an evolutionary consequence of interactions between the dentition and food, and process-based models that integrate these ingredients can inform both the possible roles of certain foods as well as the potential fitness benefits of different dental morphologies or extradentary mechanical advantages. This may be particularly informative if multiple hominin species were conspecifics and competing for similar resources. In the future, the mechanics employed by similar SDP models could be used to explore possible outcomes of competitive interactions between hominin species as well as the potential advantages conferred by hunting and/or technological innovations such as cooking.

Acknowledgements: We thank CE Chow, AM Kilpatrick, TS Kraft, T Levi, PW Lucas, AD Melin, GL Moritz, M Novak, AO Shelton, and ER Vogel for insightful comments and helpful discussions. This work was partially supported by a National Science Foundation (NSF) Grant 2009-0417 to MM, and a NSF graduate research fellowship to JDY.

REFERENCES

- Alberts, S. C., J. A. Hollister-Smith, R. S. Mututua, S. N. Sayialel, P. M. Muruthi, J. K.
Warutere, and J. Altmann. 2005. Seasonality and long-term change in a savanna
environment. *In* D. K. Brockman and C. P. van Schaik, eds., *Seasonality in primates:*
Studies of living and extinct human and non-human primates. Cambridge University
Press, Cambridge.
- Altmann, S. A. 2009. Fallback foods, eclectic omnivores, and the packaging problem.
American Journal of Physical Anthropology 140:615–629.
- Balter, V., J. Braga, P. Télouk, and J. F. Thackeray. 2012. Evidence for dietary change but
not landscape use in South African early hominins. *Nature* .
- Barbehenn, R., Z. Chen, D. Karowe, and A. Spickard. 2004. C3 grasses have higher
nutritional quality than C4 grasses under ambient and elevated atmospheric CO2.
Global Change Biology 10:1565–1575.
- Barton, R. A., A. Whiten, R. W. Byrne, and M. English. 1993. Chemical composition of
baboon plant foods: implications for the interpretation of intra- and interspecific
differences in diet. *Folia Primatologia* 61:1–20.
- Belovsky, G. 1988. An optimal foraging-based model of hunter-gatherer population
dynamics. *Journal of Anthropological Archaeology* 7:329–372.
- Boccaro, N. 2004. *Modeling complex systems.* Springer, New York.
- Boutton, T., G. Cameron, and B. Smith. 1978. Insect herbivory on C3 and C4 grasses.
Oecologia 36:21–32.
- Boyer, D., G. Ramos-Fernandez, O. Miramontes, J. L. Mateos, G. Cocho, H. Larralde,
H. Ramos, and F. Rojas. 2006. Scale-free foraging by primates emerges from their

interaction with a complex environment. Proceedings of the Royal Society of London
594 Series B-Biological Sciences 273:1743–1750.

Bronikowski, A. M., J. Altmann, D. K. Brockman, M. Cords, L. M. Fedigan, A. Pusey,
596 T. Stoinski, W. F. Morris, K. B. Strier, and S. C. Alberts. 2011. Aging in the natural
world: comparative data reveal similar mortality patterns across primates. Science
598 331:1325–1328.

Caswell, H., F. Reed, S. N. Stephenson, and P. Werner. 1973. Photosynthetic pathways and
600 selective herbivory: a hypothesis. The American Naturalist 107:465–480.

Cerling, T. E., E. Mbua, F. M. Kirera, F. K. Manthi, F. E. Grine, M. G. Leakey,
602 M. Sponheimer, and K. T. Uno. 2011. Diet of *Paranthropus boisei* in the early
Pleistocene of East Africa. Proceedings of the National Academy of Sciences of the
604 USA 108:9337–9341.

Clark, C. W., and M. Mangel. 2000. Dynamic state variable models in ecology: methods
606 and applications. Oxford University Press, USA.

Constantino, P. J. 2013. The "Robust" Australopiths. Nature Education Knowledge 4:1.

608 Constantino, P. J., J. J. W. Lee, H. Chai, B. Zipfel, C. Ziscovici, B. R. Lawn, and P. W.
Lucas. 2010. Tooth chipping can reveal the diet and bite forces of fossil hominins.
610 Biology Letters 6:826–829.

Copeland, S. 2004. Paleoanthropological implications of vegetation and wild plant resources
612 in modern savanna landscapes, with applications to Plio-Pleistocene Olduvai Gorge,
Tanzania. Ph.D. thesis. Rutgers University.

614 Dominy, N. J. 2012. Hominins living on the sedge. Proceedings of the National Academy of
Sciences of the USA 109:20171–20172.

- Dominy, N. J., E. R. Vogel, J. D. Yeakel, P. J. Constantino, and P. W. Lucas. 2008. Mechanical properties of plant underground storage organs and implications for dietary models of early hominins. *Evolutionary Biology* 35:159–175.
- Dunbar, R. I. M. 2005. Socioecology of the extinct theropiths: a modelling approach. *In Theropithecus: the rise and fall of a primate genus*. Cambridge University Press, Cambridge.
- Galbany, J., J. Altmann, A. Pérez-Pérez, and S. C. Alberts. 2011. Age and individual foraging behavior predict tooth wear in Amboseli baboons. *American Journal of Physical Anthropology* 144:51–59.
- Griffith, C., and B. Long. 2010. HOMINIDS: An agent-based spatial simulation model to evaluate behavioral patterns of early Pleistocene hominids. *Ecological Modelling* 221:738–760.
- Grine, F. E., M. Sponheimer, P. S. Ungar, J. Lee-Thorp, and M. F. Teaford. 2012. Dental microwear and stable isotopes inform the paleoecology of extinct hominins. *American Journal of Physical Anthropology* 148:285–317.
- Henry, A. G., P. S. Ungar, B. H. Passey, M. Sponheimer, L. Rossouw, M. Bamford, P. Sandberg, D. J. de Ruiter, and L. Berger. 2012. The diet of *Australopithecus sediba*. *Nature* 487:90–93.
- Houston, A., and J. M. McNamara. 1999. Models of adaptive behaviour. Cambridge University Press, Cambridge.
- Janssen, M., J. Sept, and C. Griffith. 2007. Hominids foraging in a complex landscape: Could *Homo ergaster* and *Australopithecus boisei* meet their calories requirements? Takahashi, S., Sallach, D., & Rouchier, J.(Eds.), *Advancing Social Simulation*. Springer Publishing pages 307–318.

640 Jolly, C. J. 1970. The seed-eaters: a new model of hominid differentiation based on a
baboon analogy. *Man* 5:1–26.

642 Juanes, F. 1992. Why do decapod crustaceans prefer small-sized molluscan prey? *Marine
Ecology Progress Series* 87:239–239.

644 Juanes, F., and L. Smith. 1995. The ecological consequences of limb damage and loss in
decapod crustaceans: a review and prospectus. *Journal of Experimental Marine
646 Biology and Ecology* 193:197–223.

Kay, R. F. 1981. The nut-crackers: A new theory of the adaptations of the Ramapithecinae.
648 *American Journal of Physical Anthropology* 55:141–151.

———. 1985. Dental evidence for the diet of *Australopithecus*. *Annual Review of
650 Anthropology* 14:315–341.

King, S. J., S. J. Arrigo-Nelson, S. T. Pochron, G. M. Semperebon, L. R. Godfrey, P. C.
652 Wright, and J. Jernvall. 2005. Dental senescence in a long-lived primate links infant
survival to rainfall. *Proceedings of the National Academy of Sciences of the USA*
654 102:16579–16583.

Koch, P. L. 2007. Isotopic study of the biology of modern and fossil vertebrates. Pages
656 99–154 *in* R. Michener and K. Lajtha, eds. *Stable Isotopes in Ecology and
Environmental Science*. Blackwell Publishing, Boston.

658 Laden, G., and R. Wrangham. 2005. The rise of the hominids as an adaptive shift in
fallback foods: plant underground storage organs (USOs) and australopith origins.
660 *Journal of Human Evolution* 49:482–498.

Lee-Thorp, J. 2011. The demise of "Nutcracker Man". *Proceedings of the National
662 Academy of Sciences of the USA* 108:9319–9320.

Lee-Thorp, J., A. Likius, H. T. Mackaye, P. Vignaud, M. Sponheimer, and M. Brunet. 2012.

Isotopic evidence for an early shift to C4 resources by Pliocene hominins in Chad.

Proceedings of the National Academy of Sciences of the USA 109:20369–20372.

Leonard, W., and M. Robertson. 1997. Comparative primate energetics and hominid evolution. American Journal of Physical Anthropology 102:265–281.

Levi, T., F. Lu, D. Yu, and M. Mangel. 2011. The behaviour and diet breadth of central-place foragers: an application to human hunters and Neotropical game management. Evolutionary Ecology Research 13:171–185.

Lindstedt, S. L., and W. A. Calder III. 1981. Body size, physiological time, and longevity of homeothermic animals. Quarterly Review of Biology 56:1–16.

Lockwood, C. A., C. G. Menter, J. Moggi-Cecchi, and A. W. Keyser. 2007. Extended male growth in a fossil hominin species. Science 318:1443–1446.

Lucas, P. W. 2004. Dental functional morphology: How teeth work. Cambridge University Press, Cambridge.

Lucas, P. W., P. J. Constantino, and B. A. Wood. 2008*a*. Inferences regarding the diet of extinct hominins: structural and functional trends in dental and mandibular morphology within the hominin clade. Journal of Anatomy 212:486–500.

Lucas, P. W., P. J. Constantino, B. A. Wood, and B. R. Lawn. 2008*b*. Dental enamel as a dietary indicator in mammals. BioEssays 30:374–385.

Lucas, P. W., R. Omar, K. Al-Fadhalah, A. S. Almusallam, A. G. Henry, S. Michael, L. A. Thai, J. Watzke, D. S. Strait, and A. G. Atkins. 2012. Mechanisms and causes of wear in tooth enamel: implications for hominin diets. Journal of The Royal Society Interface 10:20120923–20120923.

- 686 Lucas, P. W., I. M. Turner, N. J. Dominy, and N. Yamashita. 2000. Mechanical defences to
herbivory. *Annals of Botany* 86:913–920.
- 688 Macho, G. A. 1999. Effects of loading on the biochemical behavior of molars of *Homo*, *Pan*,
and *Pongo*. *American Journal of Physical Anthropology* 109:211–227.
- 690 Mangel, M., and C. W. Clark. 1988. *Dynamic modeling in behavioral ecology*. Princeton
University Press, Princeton.
- 692 Mangel, M., and D. Ludwig. 1992. Definition and evaluation of the fitness of behavioral and
developmental programs. *Annual Review of Ecology and Systematics* 23:507–536.
- 694 Marlowe, F. W. 2003. A critical period for provisioning by Hadza men implications for pair
bonding. *Evolution and Human Behavior* 24:217–229.
- 696 Marlowe, F. W., and J. C. Berbesque. 2009. Tubers as fallback foods and their impact on
Hadza hunter-gatherers. *American Journal of Physical Anthropology* 140:751–758.
- 698 McArthur, C., and G. D. Sanson. 1988. Tooth wear in eastern grey kangaroos (*Macropus*
giganteus) and western grey kangaroos (*Macropus fuliginosus*), and its potential
700 influence on diet selection, digestion and population parameters. *Journal of Zoology*
215:491–504.
- 702 McGraw, W. S., and D. J. Daegling. 2012. Primate Feeding and Foraging: Integrating
Studies of Behavior and Morphology. *Annual Review of Anthropology* 41:203–219.
- 704 McGraw, W. S., J. D. Pampush, and D. J. Daegling. 2012. Brief communication: Enamel
thickness and durophagy in mangabeys revisited. *American Journal of Physical*
706 *Anthropology* 147:326–333.
- Milton, K. 1989. Primate diets and gut morphology: implications for hominid evolution.

708 *In* Food and evolution: toward a theory of human food habits. Temple University
Press, Philadelphia.

710 Organ, C., C. L. Nunn, Z. Machanda, and R. W. Wrangham. 2011. Phylogenetic rate shifts
in feeding time during the evolution of *Homo*. Proceedings of the National Academy
712 of Sciences of the USA 108:14555–14559.

Osborne, J. W. 1981. Ageing. Pages 352–356 *in* A. H. R. Rowe and R. B. Johns, eds.

714 Dental Anatomy and Embryology Vol. 2: A comparison to dental studies. Blackwell,
Oxford.

716 Pate, J. S., and K. W. Dixon. 1982. Tuberous, cormous and bulbous plants. Biology of an
adaptive strategy in Western Australia. University of Western Australia Press. .

718 Perez-Barberia, F. J., and I. J. Gordon. 1998. The influence of molar occlusal surface area
on the voluntary intake, digestion, chewing behaviour and diet selection of red deer
720 (*Cervus elaphus*). Journal of Zoology 245:307–316.

Pinder III, J. E., and G. C. Kroh. 1987. Insect herbivory and photosynthetic pathways in
722 old-field ecosystems. Ecology 68:254–259.

Post, D. G. 1982. Feeding behavior of yellow baboons (*Papio cynocephalus*) the Amboseli
724 National Park, Kenya. International Journal of Primatology 3:403–430.

Procheş, Ş., R. M. Cowling, P. Goldblatt, J. C. Manning, and D. A. Snijman. 2006. An
726 overview of the Cape geophytes. Biological Journal of the Linnean Society 87:27–43.

Rabenold, D., and O. M. Pearson. 2011. Abrasive, silica phytoliths and the evolution of
728 thick molar enamel in primates, with implications for the diet of *Paranthropus boisei*.
PLoS ONE 6:e28379.

- 730 Raupp, M. J. 1985. Effects of leaf toughness on mandibular wear of the leaf beetle,
Plagioder a versicolora. *Ecological Entomology* 10:73–79.
- 732 Research, W. 2012. Wolfram—KnowledgeBase. Wolfram Research, Inc, Champaign, Illinois.
- Roitberg, B. D., D. R. Gillespie, D. M. J. Quiring, C. R. Alma, W. H. Jenner, J. Perry,
734 J. H. Peterson, M. Salomon, and S. VanLaerhoven. 2005. The cost of being an
omnivore: mandible wear from plant feeding in a true bug. *Die Naturwissenschaften*
736 92:431–434.
- Rothman, J. M., D. Raubenheimer, and C. A. Chapman. 2011. Nutritional geometry:
738 gorillas prioritize non-protein energy while consuming surplus protein. *Biology*
Letters 7:847–849.
- 740 Sayers, K., M. A. Norconk, and N. L. Conklin-Brittain. 2010. Optimal foraging on the roof
of the world: Himalayan langurs and the classical prey model. *American Journal of*
742 *Physical Anthropology* 141:337–357.
- Schoeninger, M. J., H. T. Bunn, S. S. Murray, and J. A. Marlett. 2001. Composition
744 of tubers used by hadza foragers of Tanzania. *Journal of Food Composition and*
Analysis 14:15–25.
- 746 Shellis, R. P., A. D. Beynon, D. J. Reid, and K. M. Hiiemae. 1998. Variations in molar
enamel thickness among primates. *Journal of Human Evolution* 35:507–522.
- 748 Skogland, T. 1988. Tooth wear by food limitation and its life history consequences in wild
reindeer. *Oikos* 51:238–242.
- 750 Sponheimer, M., and J. Lee-Thorp. 1999. Isotopic evidence for the diet of an early hominid,
Australopithecus africanus. *Science* 283:368.

- 752 ———. 2003. Differential resource utilization by extant great apes and australopithecines:
towards solving the C4 conundrum. *Comparative Biochemistry and Physiology, Part*
754 *A* 136:27–34.
- Sponheimer, M., J. Lee-Thorp, D. de Ruiter, D. Codron, J. Codron, A. Baugh, and
756 F. Thackeray. 2005. Hominins, sedges, and termites: new carbon isotope data from
the Sterkfontein valley and Kruger National Park. *Journal of Human Evolution*
758 48:301–312.
- Sponheimer, M., J. E. Loudon, D. Codron, M. E. Howells, J. D. Pruett, J. Codron, D. J.
760 de Ruiter, and J. A. Lee-Thorp. 2006. Do “savanna” chimpanzees consume C4
resources? *Journal of Human Evolution* 51:128–133.
- 762 Stirling, I. 1969. Tooth wear as a mortality factor in the Weddell seal, *Leptonychotes*
weddelli. *Journal of Mammalogy* 50:559–565.
- 764 Swennen, C., L. De Bruijn, P. Duiven, M. Leopold, and E. Martijn. 1983. Differences
in bill form of the oystercatcher *Haematopus ostralegus*; a dynamic adaptation to
766 specific foraging techniques. *Netherlands Journal of Sea Research* 17:57–83.
- Teaford, M. F., and O. J. Oyen. 1989. Differences in the rate of molar wear between
768 monkeys raised on different diets. *Journal of Dental Research* 68:1513–1518.
- Ungar, P. S., F. E. Grine, and M. F. Teaford. 2008. Dental microwear and diet of the
770 Plio-Pleistocene hominin *Paranthropus boisei*. *PLoS ONE* 3:e2044.
- Ungar, P. S., R. S. Scott, F. E. Grine, and M. F. Teaford. 2010. Molar microwear
772 textures and the diets of *Australopithecus anamensis* and *Australopithecus afarensis*.
Philosophical Transactions of the Royal Society B: Biological Sciences 365:3345–3354.
- 774 Ungar, P. S., and M. Sponheimer. 2011. The diets of early hominins. *Science* 334:190–193.

Vincent, A. S. 1985. Plant foods in savanna environments: a preliminary report of tubers
eaten by the Hadza of Northern Tanzania. *World Archaeology* 17:131–148.

Vogel, E. R., J. T. van Woerden, P. W. Lucas, S. S. Utami Atmoko, C. P. van Schaik, and
N. J. Dominy. 2008. Functional ecology and evolution of hominoid molar enamel
thickness: *Pan troglodytes schweinfurthii* and *Pongo pygmaeus wurmbii*. *Journal of*
Human Evolution 55:60–74.

Weishampel, D. B., P. Dodson, and H. Osmólska. 2004. *The Dinosauria*. University of
California Press, Berkeley.

White, T. D., B. Asfaw, Y. Beyene, Y. Haile-Selassie, C. O. Lovejoy, G. Suwa, and
G. Woldegabriel. 2009. *Ardipithecus ramidus* and the paleobiology of early hominids.
Science 326:64–64, 75–86.

Williams, S. H., B. W. Wright, V. d. Truong, C. R. Daubert, and C. J. Vinyard. 2005.
Mechanical properties of foods used in experimental studies of primate masticatory
function. *American Journal of Primatology* 67:329–346.

Wood, B. A., and P. J. Constantino. 2007. *Paranthropus boisei*: Fifty years of evidence and
analysis. *American Journal of Physical Anthropology* 134:106–132.

Wood, B. A., and K. Schroer. 2012. Reconstructing the diet of an extinct hominin taxon:
the role of extant primate models. *International Journal of Primatology* 33:716–742.

Yeakel, J. D., N. C. Bennett, P. L. Koch, and N. J. Dominy. 2007. The isotopic ecology of
African mole rats informs hypotheses on the evolution of human diet. *Proceedings*
of the Royal Society of London Series B-Biological Sciences 274:1723–1730.

Youngblood, D. 2004. Identifications and quantification of edible plant foods in the Upper
(Nama) Karoo, South Africa. *Economic Botany* 58:S43–S65.

Figures

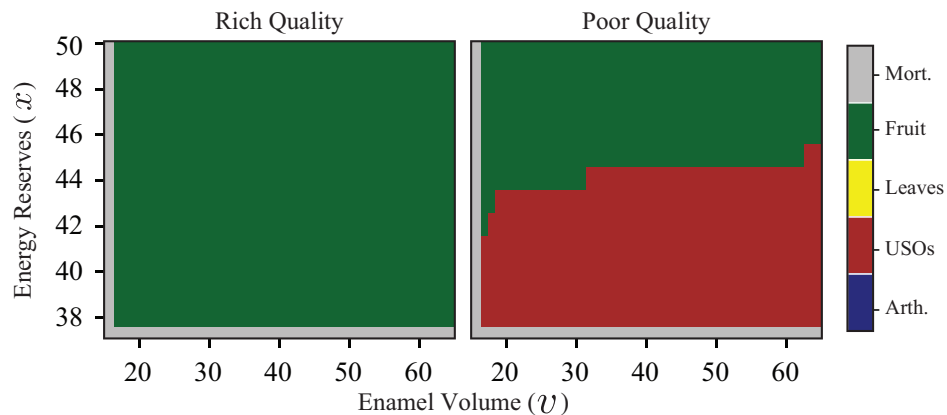


Fig. 1.— Stationary solutions to the fitness-maximizing equations $F_r(x, v)$ (rich quality habitat) and $F_p(x, v)$ (poor quality habitat) for a 50 kg anthropoid primate with no mechanical advantages. There are no differences between wet, dry, or autocorrelated conditions. Gray elements denote values of (x, v) resulting in mortality.

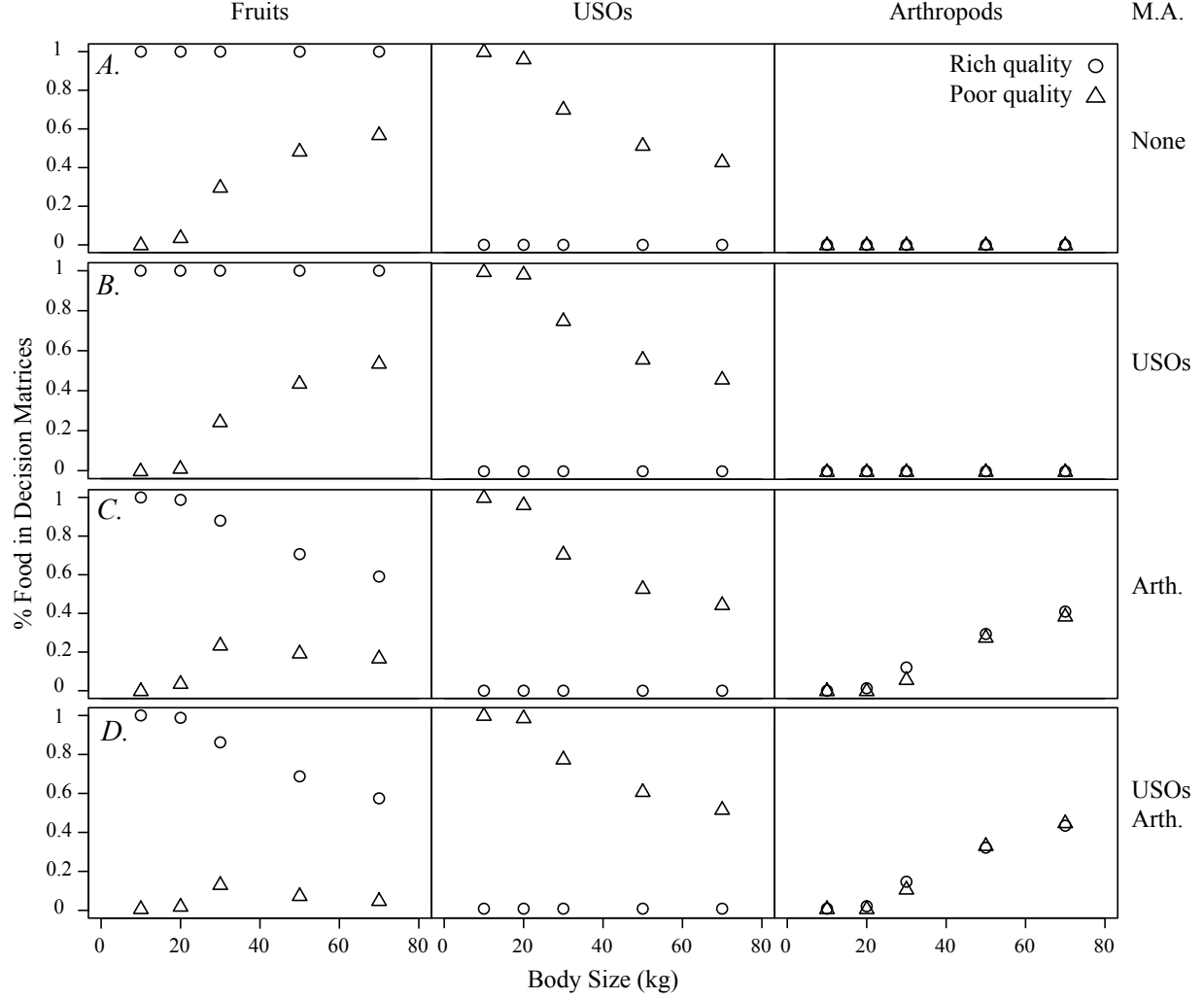


Fig. 2.— The proportional contribution of foods to the decision matrices of anthropoid primates with body sizes ranging from 10 to 70 kg. Contributions of foods for the no mechanical advantage scenario (A.) the USO advantage scenario (B.), the arthropod advantage scenario (C.), and the arthropod + USO advantage scenario (D.). Grass leaves are not found to be optimal foraging solutions in any decision matrix. Results are shown for the autocorrelated environment scenario; results for wet and dry scenarios were qualitatively similar.

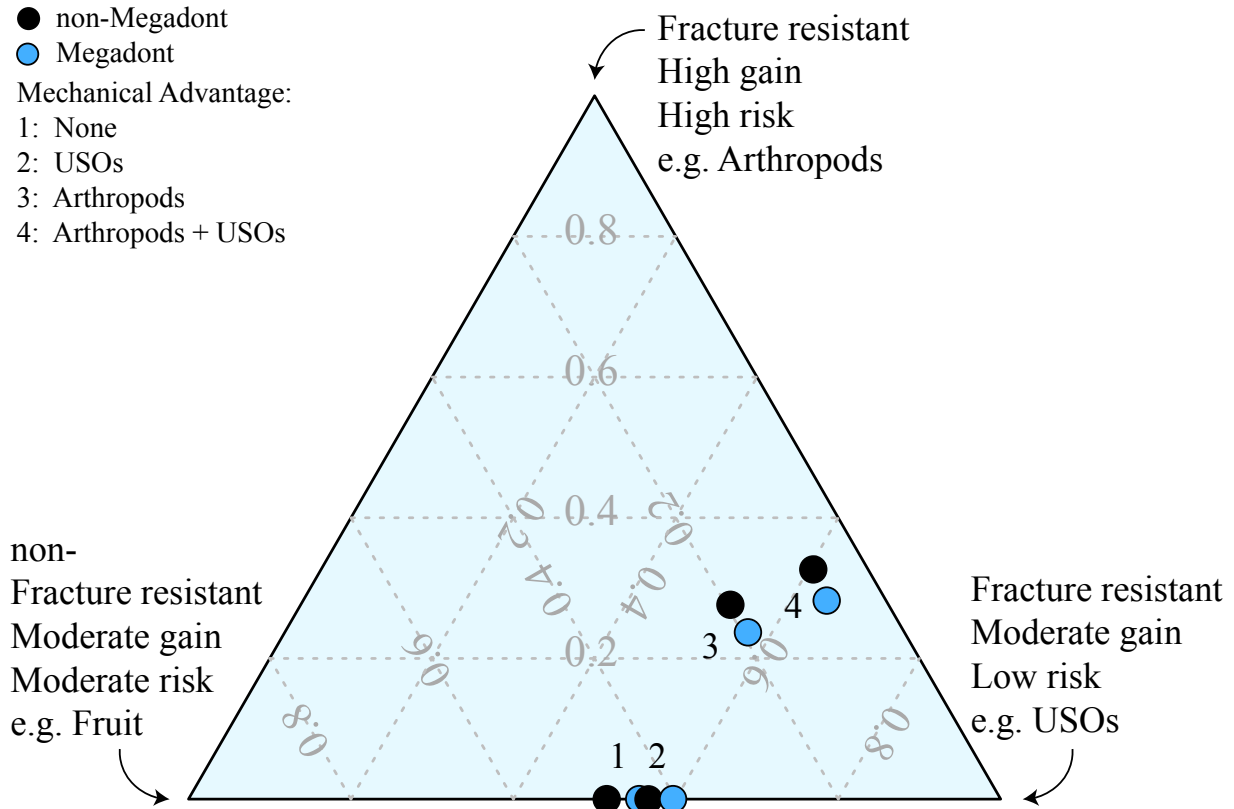


Fig. 3.— Ternary diagram showing the proportional contribution of fruit, USOs, and arthropods to the decision matrices of both 50 kg non-megadont and megadont primates under each mechanical advantage scenario. Results are shown for the autocorrelated environment scenario; results for wet and dry scenarios were qualitatively similar.

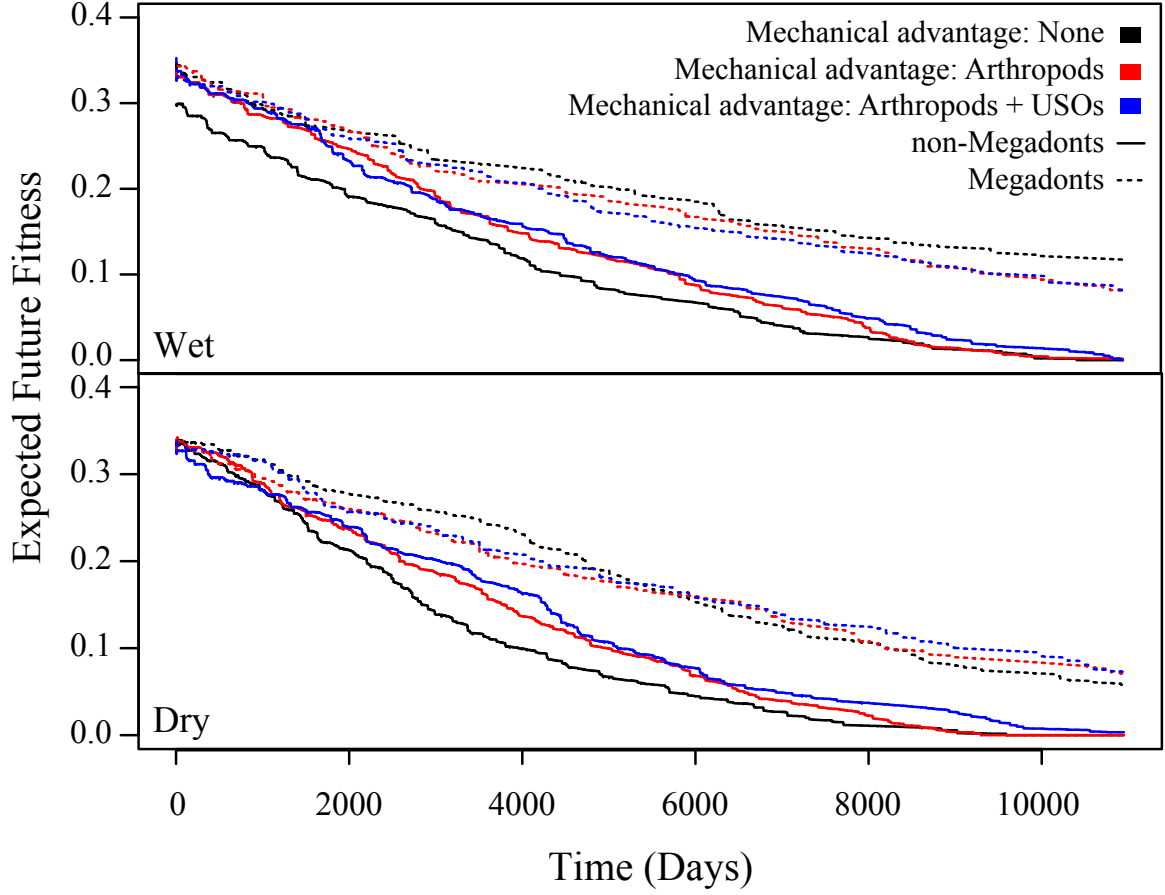


Fig. 4.— Expected fitness trajectories for $N = 100$ 50 kg non-megadont (solid) and megadont (stippled) primates over an estimated lifespan with varying mechanical advantages (none, arthropods, arthropods + USOs), during both wet and dry environmental conditions.

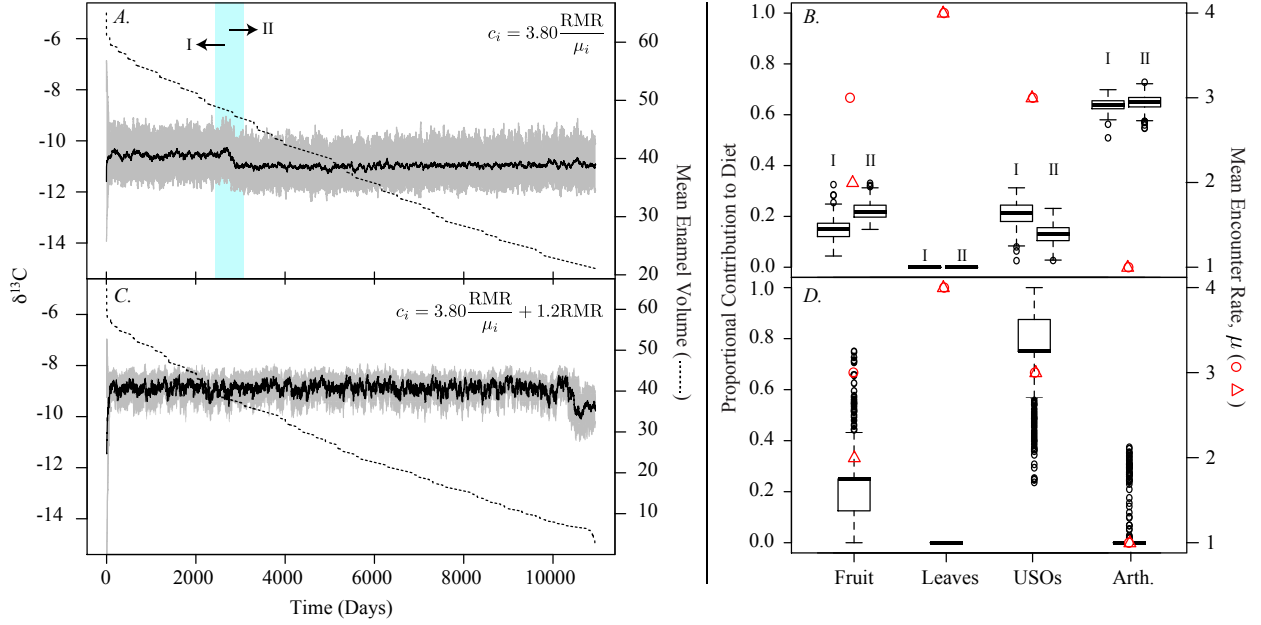


Fig. 5.— Forward simulation of the $\delta^{13}\text{C}$ values (black line denotes running mean; gray band denotes maximum and minimum value), mean enamel volume, and the proportional contribution of food-items to the diets of $N = 100$, 50 kg individuals foraging in a dry environment over an estimated lifespan. *A.* and *B.* When foraging costs are minimal, a dietary switch is observed to occur near day 3500, and labels I and II denote the pre- and post-diet switch. *C.* and *D.* The same simulation when foraging costs are elevated. In panels *B.* and *D.*, the red circles and triangles denote the mean encounter rate for each food in rich quality and poor quality habitats, respectively.

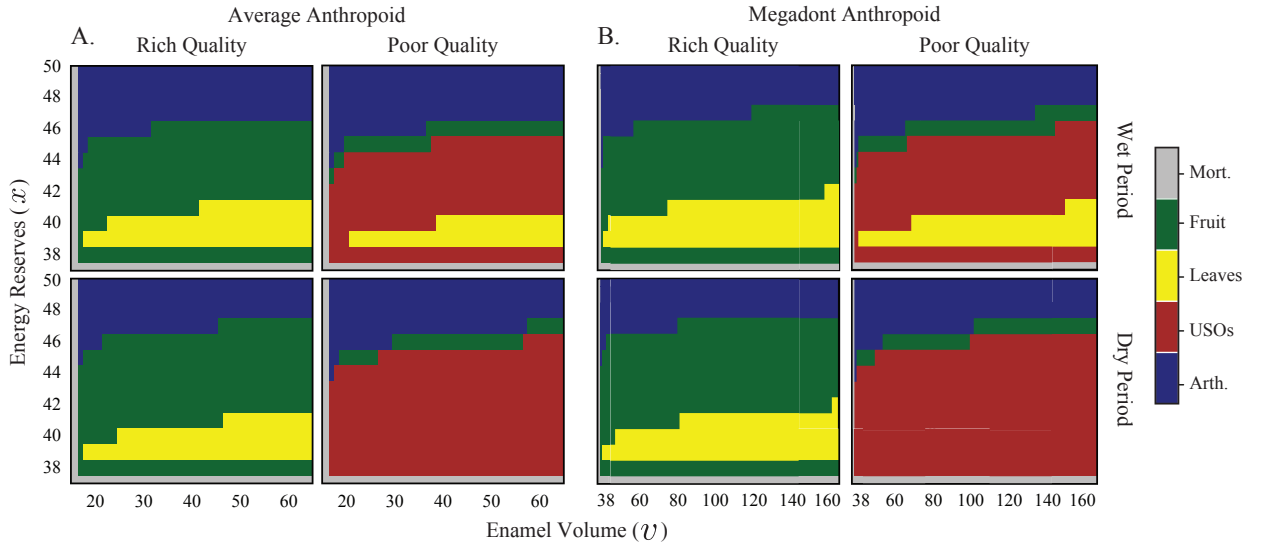


Fig. 6.— Stationary solutions for the fitness-maximizing equations, $F_r(x, v)$ and $F_p(x, v)$, as a function of energy reserves x and enamel volume v for both non-megadont and megadont primates when grass leaves are hyper-abundant and for the arthropod + USO mechanical advantage scenario. Gray elements denote values of (x, v) resulting in mortality.

Parameter	Interpretation	Units	Value(s): Rich quality	Poor quality
$X(t) = x$	Energy reserves at time t	10 [MJ]	State Variable	
$V(t) = v$	Enamel volume at time t	100 [mm ³]	State Variable	
$K = k$	Number of food items found	Count	Stochastic Variable	
$\Omega = \omega$	Basal enamel wear	[mm]	Stochastic Variable	
γ	Energetic Gain	10 [MJ]	(1.5, 0.3, 1.6, 3.2)	(1.4, 0.3, 1.4, 2.9)
c	Energetic Cost (minimal)	10 [MJ]	(0.7, 0.5, 0.7, 2.2)	(1.1, 0.5, 0.7, 2.2)
	Energetic Cost (maximal)	10 [MJ]	(1.4, 1.2, 1.4, 2.8)	(1.8, 1.2, 1.4, 2.8)
ξ	Mean encounter rate	time ⁻¹	(3, 4, 3, 1)	(2, 4, 3, 1)
ν	Dispersion	NA	(3, 5, 3, 2)	(2, 4, 3, 1)
η	Digestibility	NA	(0.9, 0.7, 0.8, 0.9)	Same
A	Molar surface area	[mm ²]	$\sum_{m=1}^3 \pi L_m^2$	Same
b	Slope of enamel wear	[mm/k]	0.0425	Same
E	Young's modulus	[MPa]	(1, 11, 5, 200)	Same
R	Fracture toughness	[Jm ⁻²]	(565, 300, 265, 1345)	Same
$\bar{\omega}$	Expected basal enamel wear	μm	0.24	Same
σ	Basal enamel wear SD	μm	1.6	Same
d	Prob. of death at time t	NA	4.54×10^{-5}	Same
$Q(t)$	Habitat quality at time t	NA	r	p
ρ	Quality transition probability matrix: $(\rho_{rr}, \rho_{rp}; \rho_{pr}, \rho_{pp})$		Wet (0.8, 0.2; 0.2, 0.8) Dry (0.2, 0.8; 0.8, 0.2) Auto. (0.8, 0.2; 0.8, 0.2)	
Φ	Terminal fitness function ($t = T$)			
F	Fitness function ($t < T$)			
$D^*(x, v)$	Stationary decision matrix			
\hat{F}	Expected future fitness			

Table 1: Parameters and variables in the dynamic state variable model. Parenthetical values (except for ρ) refer to those for foods: (fruit, grass leaves, USOs, arthropods). Values for E and R are those when no mechanical advantage is included. See methods for relevant references. Auto. = Autocorrelated.